

The origin of the Australian Vespertilioninae bats, as indicated by chromosomal studies

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Abstract

Two species of Australian vespertilionids were karyologically studied, *Falsistrellus tasmaniensis* and *Scotorepens balstoni*. The *Falsistrellus* karyotype is composed of 44 chromosomes and, apart from some minor differences, is identical with those of other Australian Vespertilioninae described previously. *Scotorepens balstoni* displays a unique karyotype consisting of 30 chromosomes.

All Australian Vespertilioninae examined so far share an altered chromosome 11, which when compared with several vespertilionid genera has been shown to represent the derived state and to be a synapomorphic feature of the tribe Vespertilionini. Therefore, the genera *Nyctophilus*, *Chalinolobus*, *Falsistrellus*, *Scotorepens* and the *Pipistrellus* subgenus *Vespadelus*, which are restricted to Australia and New Guinea, belong to the Vespertilionini tribe. Because true members of the genus *Pipistrellus* do not belong to this tribe, the elevation of the subgenus *Vespadelus* to the generic level is proposed. The close phylogenetic relationships of the morphologically rather distinct genera, together with their limited distribution, point to a common origin of all Australian Vespertilioninae, followed by adaptive radiation.

Introduction

During the last decade, several studies dealing with morphometric or electrophoretic data of Australian vespertilionids have been published. These studies have resulted in e.g. descriptions of new species or changes in generic status, raising the number of Australian vespertilionid species to 34, belonging to 11 genera. These changes in systematic position of Australian genera are briefly summarized below.

For a long time, because of their dental formula, the smallest Australian "pipistrelloid" species have been placed in the genus *Eptesicus*. The number of recognized species in this group was considerably enlarged by a morphological approach, supported by electrophoretic studies (KITCHENER et al. 1987; ADAMS et al. 1987). Due to the shape of the bacula, HILL and HARRISON (1987) transferred the Australian "*Eptesicus*" to a separate subgenus of *Pipistrellus*, i.e. *Vespadelus*. In a previous study we supported this view (VOLLETH and TIDEMANN 1989). However, additional chromosomal data obtained in the meantime (VOLLETH 1989) and the results of the present paper support the elevation of *Vespadelus* to the generic rank.

The large-sized *Pipistrellus tasmaniensis*, now considered to consist of two distinct species (*tasmaniensis*, *mackenziei*), has been shown to be phenetically and phylogenetically quite distinct from the Australian members of "*Pipistrellus tenuis*", which themselves have been split into two species restricted to Australia (*P. westralis*, *P. adamsi*; KITCHENER et al. 1986). Therefore, KITCHENER et al. (1986) resurrected *Falsistrellus* Troughton, 1943 as the generic name for *tasmaniensis* and *mackenziei*.

Because of morphological similarities *Nyctophilus* was once thought to be closely allied to the New World genus *Antrozous*; both were regarded as members of the subfamily Nyctophilinae (MILLER 1970; TATE 1942). KOOPMAN (1984), however, removed *Antro-*

zous and changed the status of the subfamily into a tribe, Nyctophilini, placed within the Vespertilioninae.

The Australian members of the Nycticeini have formerly been placed with *Scotophilus* and *Scoteinus* (for references see KITCHENER and CAPUTI 1985). Since the study of LAURIE and HILL (1954), they have been referred to the genus *Nycticeius*, which also includes species living in Africa and North America. After morphometric studies, involving several members of the tribe, KITCHENER and CAPUTI (1985) placed the Australian species into two distinct endemic genera, *Scotorepens* and *Scoteanax*, erected by TROUGHTON (1943).

This paper deals with chromosomal data of two endemic species, *Falsistrellus tasmaniensis* (Gould, 1858) and *Scotorepens balstoni* (THOMAS 1906). The results, together with those of a previously published study (VOLLETH and TIDEMANN 1989), enable us to suppose that three quarters of the Australian vespertilionid species have evolved from a common ancestor. This adaptive radiation is comparable, although with considerably fewer species involved, with the radiation of the Corvi (Passeres, Aves) during the Tertiary in Australia (SIBLEY and AHLQUIST 1985).

Materials and methods

The animals were collected from free-living populations in 1989. The specimens are deposited in the Senckenberg-Museum, Frankfurt/Main (SMF) (accession numbers in parentheses).

Specimens examined: *Falsistrellus tasmaniensis* (Gould, 1858), Bull's Head, Australian Capital Territory, 34° 24' S, 148° 50' E (male, SMF 77897); *Scotorepens balstoni* (Thomas 1906), Double Tanks, Willandra Lakes Region, New South Wales, 33° 42' S, 142° 54' E (two males, SMF 77898 and 77899).

Metaphases were obtained from fibroblast cultures of heart and lung biopsies. Culture conditions as well as chromosome preparation and staining procedures are described elsewhere (see VOLLETH and TIDEMANN 1989). For the calculation of the FN (fundamental number) completely heterochromatic arms have not been taken into account. The chromosome arms were numbered according to BICKHAM (1979a). Comparison of the G-banding pattern of *Myotis* with those of other vespertilionid genera revealed clear differences in eight chromosomes caused by peri- or paracentric inversions. The chromosome present in *Myotis* was called "state I" and the homologous chromosome in another genus, if altered by an inversion, was called "state II" of the chromosome in question. These differences (state I vs. state II) were used as characters for an evaluation of the intergeneric relationships of the Vespertilionidae (VOLLETH 1989).

Results

Falsistrellus tasmaniensis (2n = 44, FN = 52)

This species possesses a karyotype with 44 chromosomes, composed of three large and one small metacentric and 17 acrocentric autosomal pairs. A G-banded karyotype is shown in Fig. 1.

Compared to the G-banding pattern of *Myotis* (BICKHAM 1979a), differences were found on chromosomes 1/2, 11, 12, 15 and the X, here all present in state II, as is the case with other Australian species, e.g. *Chalinolobus morio* (see VOLLETH and TIDEMANN 1989). Chromosome 7, however, shows an euchromatic short arm, clearly visible in CBG-banded metaphases (Fig. 2a), as in *Myotis* and *Vespadelus vulturinus* and *darlingtoni* (VOLLETH and TIDEMANN 1989, the species *sagittula* studied in that paper was synonymized with *darlingtoni* by KITCHENER et al. 1987). Some of the CBG-banded metaphases showed a weak interstitial heterochromatic band in the proximal region of chromosome 6 (Fig. 2a). One of the two smallest chromosome pairs (i.e. 24, 25) has acquired a large amount of heterochromatic material. One arm of the resulting banded chromosome is completely heterochromatic and of the size of arm 18; the second arm consists of euchromatic material in the proximal part (presumably the material of arm 25) and of C-

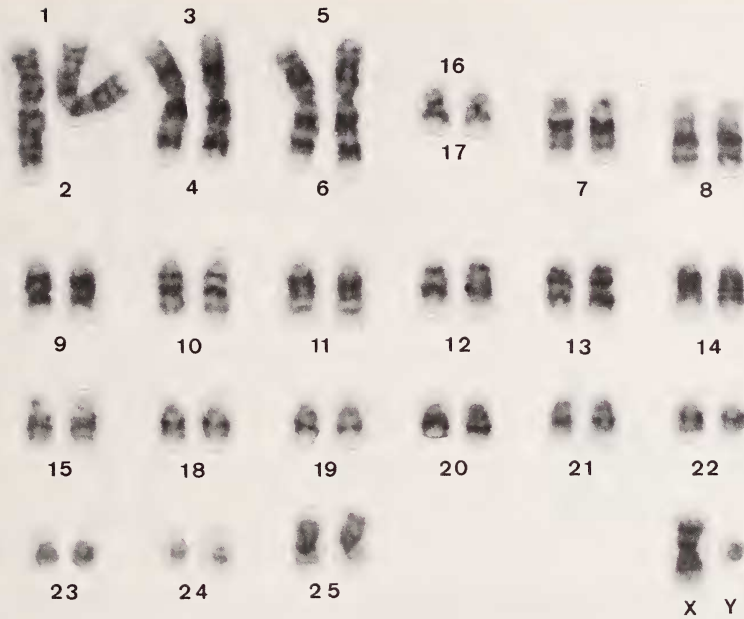


Fig. 1. G-banded karyotype of a male *Falsistrellus tasmaniensis*

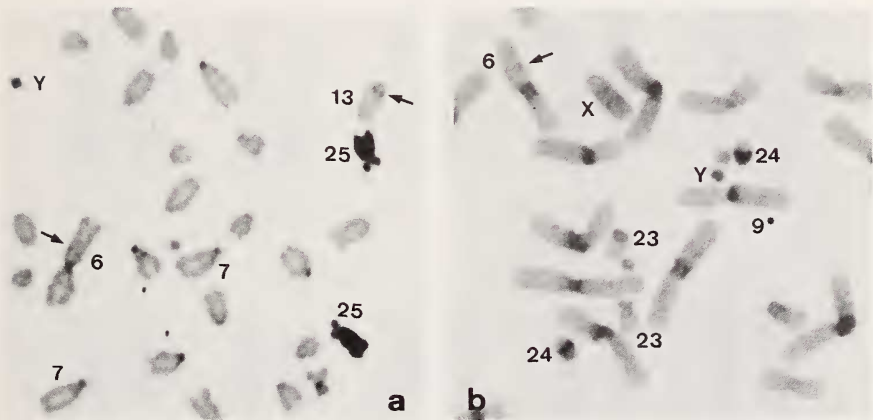


Fig. 2. Partially C-banded metaphases of *Falsistrellus tasmaniensis* (a) and *Scotorepens balstoni* (b). a: The arrows indicate faint interstitial heterochromatic bands on arm 6 and 13. Please note the tiny euchromatic short arm on chromosome 7 and the large heterochromatic blocks on chromosomes 25; b: The enlarged regions of centromeric heterochromatin on several chromosomes are clearly visible. The arrow points to the small interstitial heterochromatic band on arm 6

positive material in the distal part (Fig. 2a). The Y-chromosome is metacentric, of the same size as chromosome 24 and largely heterochromatic (Fig. 2a).

A slight difference from other vespertilionid karyotypes was found on chromosome 13. This chromosome shows two GTG-positive blocks, one proximal and one distal. In the

case of *Falsistrellus tasmaniensis* the proximal block is not, as is usually the case, divided into two subbands, but into three. The most proximal subband is very clearly separated from the others by a GTG- and QFQ-negative, and CBG-positive interband. This might be the result either of heterochromatic addition to the originally proximal situated subband or of a small paracentric inversion followed by addition of heterochromatic material.

The Nucleolus Organizer Region (NOR) is situated in the secondary constriction of chromosome 15.

Scotorepens balstoni ($2n = 30$, FN = 48)

The karyotype consists of 30 chromosomes and is composed of six large meta- to submetacentric, four medium to small submetacentric and four small acrocentric autosomal pairs. The arrangement of autosomal arms involved in banded chromosomes was traced to be 1/2, 7/4, 12/6, 13/8, 9/5, 14/11, 15/10, 21/3, and 22/20. Of the acrocentric chromosomes, arms 23, 24 and 25 were identified. The composition of two chromosomes, one submetacentric (called "A" in Fig. 3) and one acrocentric ("B"), remained unclear. Those arms, which were found to exist in two states in the Vespertilionidae, are present here in state II (1/2, 7, 11, 12, 15).

The X-chromosome is a large acrocentric and the Y-chromosome is a small metacentric chromosome. A G-banded karyotype is shown in Fig. 3.

In addition to two Robertsonian fissions and eight centric fusions, responsible for the reduction of the diploid chromosome number, one paracentric inversion (arm 1), one centromere shift (X-chromosome) and heterochromatic addition on several chromosomes occurred during the chromosomal evolution of this species. The inverted segment on

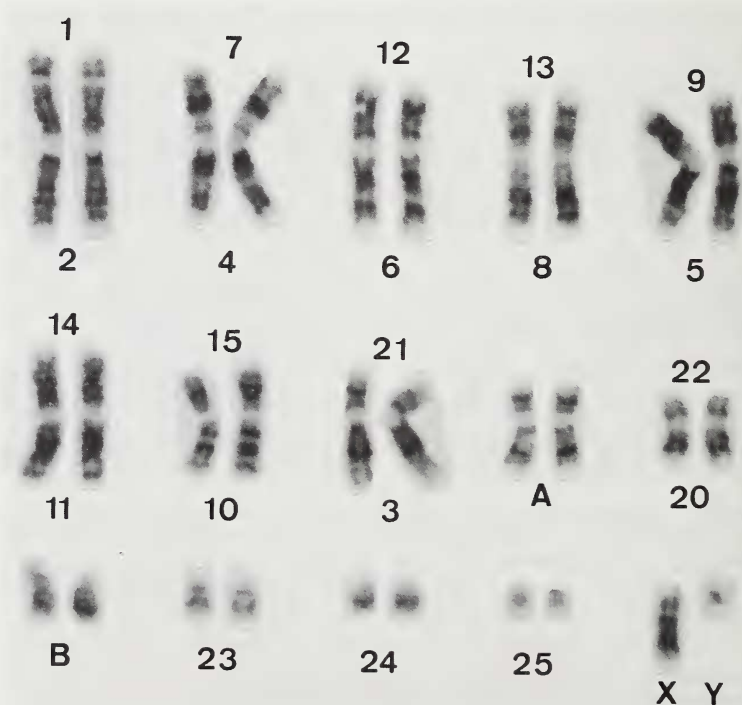


Fig. 3. G-banded karyotype of a male *Scotorepens balstoni*

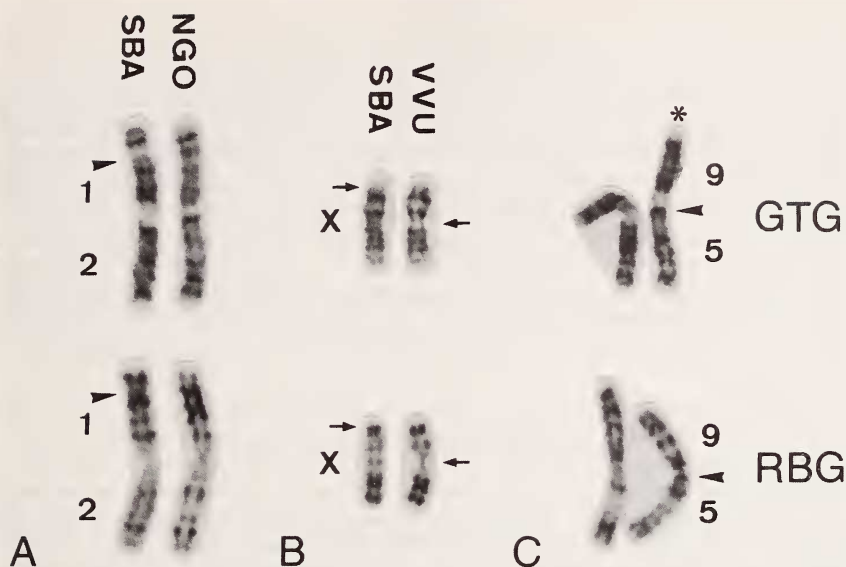


Fig. 4. Peculiar *Scotorepens balstoni* (SBA) chromosomes. Upper row: GTG-banding; lower row: replication banding (RBG). A: Chromosome 1/2 of SBA (left) compared with that of *Nyctophilus gouldi* (NGO, right). The arrow points to the proximal end of the inverted portion. B: X-chromosome compared with the X of *Vespadelus vulturnus* (VVU). The arrows indicate the position of the centromeres. C: Polymorphism on chromosome pair 9/5 in SBA. The right chromosome (indicated by a star) shows an additional segment on arm 5, close to the centromere, indicated by the arrowhead. Further explanations see text

chromosome 1/2 is located in the terminal region of arm 1, as can be clearly seen when compared with the unaltered homologous chromosome of *Nyctophilus gouldi* (Fig. 4A). The centromere shift or centromere transposition, which moved the centromere to the formerly telomere region of the short arm of the X-chromosome, can be demonstrated when the metacentric X of *Vespadelus vulturnus* is compared with it (Fig. 4B). In this case, only replication banding (RBG) is appropriate to show that the altered chromosome cannot be derived by a simple inversion. A polymorphic feature was detected on chromosome pair 9/5. Both specimens examined showed one "normal" chromosome and one with an additional segment in the proximal region of arm 5. This small segment was characterized as GTG-, RBG- and CBG-positive and CMA-negative (Fig. 4C). The origin of this segment remains unclear.

In 11 out of the total of 14 autosomal pairs the amount of centromeric heterochromatin is increased. These regions are completely GTG-negative and late replicating. They are CBG-positive and showed bright fluorescence after staining with chromomycin A. Only chromosomes 15/10, 22/20 and 25 lack these regions. As in *Falsistrellus*, a faint interstitial C-positive band was detected on arm 6 (Fig. 2b). The proximal half of the small acrocentric chromosome 24 is CBG-positive. The small Y-chromosome appears to be totally heterochromatic (Fig. 2b).

The NOR-bearing secondary constriction is situated in the long arm of chromosome 23 close to the centromere, resulting in a clear enlargement of this chromosome when compared to that of other Australian vespertilionids.

Discussion

A comparison of the karyotypes of the Australian vespertilionid genera examined so far revealed extensive complete arm homologies (see also VOLLETH and TIDEMANN 1989). With the exception of a few minor differences, the chromosomal complement is identical in *Chalinolobus*, *Nyctophilus*, *Falsistrellus* and *Vespadelus*. Small amounts of additional heterochromatic material observed in *Chalinolobus morio* and in *Falsistrellus tasmaniensis* are located on different chromosomal pairs. A common feature present in *Falsistrellus* and *Vespadelus* is the euchromatic short arm on chromosome 7, which can be derived from the chromosome present in the other Australian genera by means of a pericentric inversion.

In contrast, several chromosomal rearrangements were found in the karyotype of *Scotorepens balstoni*, leading to a diploid chromosome number of 30. Most of the chromosomal arms, however, were found to be identical with those of the above mentioned genera.

A comparative cytogenetic study of about 20 vespertilionid genera (VOLLETH 1989) revealed a small but sufficient number of features suited for karyological characterization of tribes and subfamilies. According to these results, all "pipistrellid" genera, except *Eptesicus* and *Hesperoptenus*, share two derived features, i.e. rearranged chromosomes 15 and X. These species are thus considered to belong to two closely related tribes called Vespertilionini and Pipistrellini (VOLLETH 1989). The characteristic feature of the tribe Vespertilionini is the occurrence of state II of chromosome 11, differing from state I in a paracentric inversion. All Australian species examined so far (VOLLETH and TIDEMANN 1989, this paper) show the characteristics mentioned and belong therefore to the Vespertilionini, together with e.g. the European species *Vespertilio murinus* L., 1758 and *Hypsugo savii* (Bonaparte, 1837). Thus, representatives of three of HILL and HARRISON's (1987) *Pipistrellus* subgenera, i.e. *Hypsugo*, *Vespadelus* and *Falsistrellus*, fit in the tribe Vespertilionini, not in the Pipistrellini for karyological reasons. The often discussed (HELLER and VOLLETH 1984; KITCHENER et al. 1986; MENU 1987) polyphyletic origin of the genus *Pipistrellus* is thus confirmed. As a consequence, we propose the elevation of the subgenus *Vespadelus* to generic rank, as has been the case with *Hypsugo* and *Falsistrellus* (HORACEK and HANAK 1986; KITCHENER et al. 1986). However, the systematic position of the other species included in these taxa by HILL and HARRISON (1987) should remain tentative unless they have been examined cytogenetically. As far as the systematic position of *Falsistrellus* is concerned, our results corroborate the morphological analyses of KITCHENER et al. (1986). This genus is closely related to *Vespadelus*, sharing a common feature, the short arm on chromosome 7.

The classification of the genera *Nyctophilus* and *Scotorepens* with the Vespertilionini might be surprising at first view, because of their morphological specializations. However, it seems rather improbable that the chromosomal features mentioned, which arise through relatively rare events, i.e. inversions, should have evolved independently in two or three lineages in Australia.

In contrast to *Nyctophilus*, which possesses no chromosomal peculiarities, the karyotype of *Scotorepens* shows several special features. Among them are some which could be considered as being in common with the tribe Nycticeiini. The first is the acrocentric condition of some of the chromosomal arms 1 to 6. In the Nycticeiini, either none (e.g. *Scotophilus*, *Antrozous*, BICKHAM 1979b; RUEDAS et al. 1990) or one (*Nycticeius humeralis*, BICKHAM 1979b; *Rhogeessa alleni*, VOLLETH 1989) of the original three metacentrics (1/2, 3/4, 5/6) is conserved. In *Scotorepens balstoni*, however, the remaining metacentric element is chromosome 1/2 and not 3/4 as in *Nycticeius* and *Rhogeessa alleni*. The second feature concerns the NOR-bearing secondary constriction. Except for *Scotorepens*, chromosome 15 bears the NOR in all Australian species examined so far. In *Scotorepens balstoni*, however, the NOR is located on chromosome 23 and thus on the same

chromosome as in the American *Rhogeessa alleni* (VOLLETH 1989). Because it has been shown that the location of the Nucleolus Organizer Region has changed several times in the evolution of the vespertilionids (VOLLETH 1987), we consider this feature to have evolved independently in *Rhogeessa* and *Scotorepens*. The independent occurrence of such rare events as inversions is much more unlikely. In our opinion, the genus *Scotorepens* is a member of the Vespertilionini, which acquired the Nycticeiini-like morphological features through parallel evolution. This has also been proven to be the case with the semi-arid species *Otonycteris hemprichii*, which from a karyological point of view clearly belongs to the Plecotini (ZIMA et al. 1991), but was hitherto regarded as belonging to the Nycticeiini (see e.g. KOOPMAN 1984).

Without knowledge of the karyotype, nothing can be said about the phylogenetic relationships of *Scoteanax*. Morphometric and electrophoretic studies, however, revealed that *Scoteanax rueppellii* is not as closely related to *Scotorepens* as previously thought (KITCHENER and CAPUTI 1985; BAVERSTOCK et al. 1987).

Origin of the Australian vespertilionids

The bat fauna of Australia and New Guinea shows a high degree of endemism, with 54 % of Australian bats being endemic species (HALL 1984).

Within the family Vespertilionidae, 25 of the 34 known species are confined to Australia. And only 4 of them cover a range which extends beyond New Guinea (see Table 1).

Of the vespertilionid genera occurring in Australia and/or New Guinea, 50 % have an Asian or world-wide distribution. The remaining 50 % are distributionally restricted to Australia, New Zealand, New Guinea and some small islands in the area (see Table 1). 5 of

Table 1. Distribution of Australian und New Guinean vespertilionid species

Genus	Distrib. ²	Number of endemic species			Non-endemic species ¹	
		Australia	NG	A + NG	A + NG	NG only
<i>Pipistrellus</i>	WW	2	1	—	—	3
<i>Myotis</i>	WW	—	—	—	1	—
<i>Mimiopterus</i>	OW	—	—	—	2	4
<i>Kerivoula</i>	OW	—	1	—	—	—
<i>Phoniscus</i>	AA	—	—	1	—	—
<i>Murina</i>	AA	—	—	—	1	—
<i>Philetor</i>	AA	—	—	—	—	1
<i>Nyctophilus</i>	A, NG ³	4	2	2	—	—
<i>Pharotis</i> ⁴	NG	—	1	—	—	—
<i>Chalinolobus</i>	A, NG ⁵	4	—	1	—	—
<i>Falsistrellus</i>	A	2	—	—	—	—
<i>Vespadelus</i>	A	9	—	—	—	—
<i>Scotorepens</i>	A	3	—	1	—	—
<i>Scoteanax</i> ⁴	A	1	—	—	—	—

Data taken from: STRAHAN (1983), FLANNERY (1990), KITCHENER and CAPUTI (1985), KITCHENER et al. (1986, 1987).

¹ All non-endemic species found in Australia have also been discovered in New Guinea. —
² Distribution of the genus: WW = worldwide; OW = Old World; AA = Asia plus Australia; A = Australia; NG = New Guinea. —³ One *Nyctophilus* species (*N. heran*) recently discovered on Lembata I., Indonesia (KITCHENER et al. 1991); questionable type locality of *N. timorensis* is Timor, Indonesia. —⁴ Karyological data not available. —⁵ Range of *Chalinolobus gouldii* includes New Caledonia and Norfolk I. (TIDEMANN 1986); one endemic species (*Chalinolobus tuberculatus*) occurs in New Zealand.

these 7 genera have been examined karyologically (VOLLETH and TIDEMANN 1979, this paper) and all have been found to belong to the same tribe, Vespertilionini. This close relationship in addition to the limited distribution leads to the suggestion of a common origin for all Australian Vespertilionini. Furthermore, we assume that a long period of time was required for the evolution of this tribe, which resulted in bats occupying a wide range of adaptive niches, e.g. the highly manoeuvrable foliage-cleaning *Nyctophilus*, or the genus *Scotorepens* some of which are capable of tolerating aridity. The first possibility of vespertilionids reaching Australia via Indonesia probably took place sometime in the Oligocene. At this time the ancestor of the Corvini (Aves) is thought to have moved in the opposite direction, from Australia to Asia (SIBLEY and AHLQUIST 1985). Therefore, the immigration of a few bats during the same period seems to be possible. Under favourable circumstances even small bats seem to be able to cross wide stretches of ocean, as shown by the occurrence of *Chalinolobus tuberculatus* in New Zealand and of *Chalinolobus gouldii* in New Caledonia (TIDEMANN 1986).

Several points support the view that the remaining Australian vespertilionid species, coming from Asia, perhaps via New Guinea, reached Australia considerably later, probably not earlier than during the Pliocene. These species, in contrast to the members of the endemic genera, failed to colonize the whole continent, occurring only on the northern and eastern coasts of Australia. With the exception of two endemic species of *Pipistrellus*, which are thought to have evolved independently from Papuan forms (KITCHENER et al. 1986), the remaining five Australian non-Vespertilionini species, belonging to four different subfamilies, also occur in New Guinea (see Tab. 1). In addition to *Phoniscus papuensis*, an endemic species of the Southeast-Asian genus, four widely distributed species (*Murina florium*, *Myotis adversus*, and two *Miniopterus* spp.) were successful in colonizing the region.

About the same extent of species exchange took place in the opposite direction, from Australia to New Guinea. *Chalinolobus nigrogriseus* and *Scotorepens sanborni* are thought to have reached New Guinea during the Pleistocene (FLANNERY 1990). Members of the genus *Nyctophilus*, however, must have reached New Guinea considerably earlier, probably during the Miocene (FLANNERY 1990). In addition to two species which inhabit both Australia and New Guinea, there are two *Nyctophilus* species and the related monotypic genus *Pharotis*, restricted to New Guinea. Furthermore, one recently described species, *Nyctophilus heran*, has been discovered on an Indonesian island (KITCHENER et al. 1991), adding support to Timor as the hitherto questionable type locality of *Nyctophilus timorensis*. In addition to these biogeographic peculiarities, the distribution of an ectoparasitic mite genus provides further information. In contrast to the occurrence of the same *Pteracarus* species in the vespertilionid genera *Chalinolobus*, *Scotorepens* and *Vespadelus*, the mite species parasitic on *Nyctophilus* has not been found on any other genus (FAIN and LUKOSCHUS 1979). The morphological specializations found in *Nyctophilus* and *Pharotis*, their biogeographic relationships and the evolution of a specialized ectoparasite in *Nyctophilus* support the idea of an early branching of *Nyctophilus* from the Australian Vespertilionini stock.

Too few karyological features have been found to evaluate intergeneric relationships, other than that a close affinity between *Vespadelus* and *Falsistrellus* seems highly probable. In sum, 76 % (26 species) of the Australian vespertilionids are considered to be the result of the Vespertilionini radiation and only 24 % (8 species) are made up of other vespertilionid tribes and subfamilies.

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Zusammenfassung

Die phylogenetische Herkunft der australischen Vespertilioninae nach cyto-genetischen Ergebnissen

Zwei australische Vespertilionidenarten, *Falsistrellus tasmaniensis* und *Scotorepens balstoni*, wurden cyto-genetisch untersucht. Der Karyotyp von *Falsistrellus* besteht aus 44 Chromosomen und ist bis auf geringfügige Veränderungen mit dem anderer australischer Vespertilioninae identisch. Demgegenüber ist der Chromosomensatz von *Scotorepens balstoni*, der sich aus 30 Chromosomen zusammensetzt, stärker verändert.

Ein gemeinsames Merkmal aller bislang cyto-genetisch untersuchten australischen Vespertilioninae ist ein verändertes Chromosom 11, das aufgrund einer vergleichenden Untersuchung zahlreicher anderer Gattungen (VOLLETH 1989) als abgeleitet zu betrachten ist. Aufgrund dieses Merkmals gehören die auf Australien und Neuguinea beschränkten Gattungen *Nyctophilus*, *Chalinolobus*, *Falsistrellus* und *Scotorepens* sowie die *Pipistrellus*-Untergattung *Vespadelus* alle derselben Tribus, Vespertilionini, an. Da jedoch andere Arten der Gattung *Pipistrellus* nicht zu dieser Tribus, sondern zu den Pipistrellini zu rechnen sind, wird die Anhebung des Taxons *Vespadelus* in den Rang einer Gattung vorgeschlagen. Die nahe Verwandtschaft der morphologisch sehr unterschiedlichen Gattungen weist, zusammen mit dem begrenzten Verbreitungsgebiet, auf die Abstammung von einem gemeinsamen Vorfahren und eine anschließende adaptive Radiation in Australien hin.

References

- ADAMS, M.; BAVERSTOCK, P. R.; WATTS, C. H. S.; REARDON, T. (1987): Electrophoretic resolution of species boundaries in Australian Microchiroptera. II. The *Pipistrellus* group (Chiroptera: Vespertilionidae). *Aust. J. Biol. Sci.* **40**, 163–170.
- BAVERSTOCK, P. R.; ADAMS, M.; REARDON, T.; WATTS, C. H. S. (1987): Electrophoretic resolution of species boundaries in Australian microchiroptera. III. The Nycticeini – *Scotorepens* and *Scoteanax* (Chiroptera: Vespertilionidae). *Aust. J. Biol. Sci.* **40**, 417–433.
- BICKHAM, J. W. (1979a): Banded karyotypes of 11 species of American bats (genus *Myotis*). *Cytologia* **44**, 789–797.
- (1979b): Chromosomal variation and evolutionary relationships of vespertilionid bats. *J. Mammalogy* **60**, 350–363.
- FAIN, A.; LUKOSCHUS, F. S. (1979): Parasites of Western Australia. VI. Myobiidae parasitic on bats (Acarina: Prostigmata). *Rec. West. Aust. Mus.* **7**, 61–107.
- FLANNERY, T. (1990): Mammals of New Guinea. Carina: Robert Brown and Ass.
- HALL, L. (1984): And then there were bats. In: Vertebrate zoogeography and evolution in Australia (Animals in space and time). Ed. by M. ARCHER and G. CLAYTON. Carlisle: Hesperian Press. 838–852.
- HELLER, K.-G.; VOLLETH, M. (1984): Taxonomic position of “*Pipistrellus societatis*” HILL, 1972 and the karyological characteristics of the genus *Eptesicus* (Chiroptera: Vespertilionidae). *Z. zool. Syst. Evolut.-forsch.* **22**, 65–77.
- HILL, J. E.; HARRISON, D. L. (1987): The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus*, and the descriptions of a new genus and subgenus. *Bull. Brit. Mus. (Nat. Hist.) Zool.* **52**, 225–305.
- HORACEK, I.; HANAK, V. (1986): Generic status of *Pipistrellus savii* and comments on classification of the genus *Pipistrellus* (Chiroptera: Vespertilionidae). *Myotis* **23–24**, 9–16.
- KITCHENER, D. J.; CAPUTI, N. (1985): Systematic revision of Australian *Scoteanax* and *Scotorepens* (Chiroptera: Vespertilionidae), with remarks on relationships to other Nycticeini. *Rec. West. Aust. Mus.* **12**, 85–146.
- KITCHENER, D. J.; CAPUTI, N.; JONES, B. (1986): Revision of Australo-Papuan *Pipistrellus* and of *Falsistrellus* (Microchiroptera: Vespertilionidae). *Rec. West. Aust. Mus.* **12**, 435–496.
- KITCHENER, D. J.; JONES, B.; CAPUTI, N. (1987): Revision of Australian *Eptesicus* (Microchiroptera: Vespertilionidae). *Rec. West. Aust. Mus.* **13**, 427–500.
- KITCHENER, D. J.; HOW, R. A.; MAHARADATUNKAMSI (1991): A new species of *Nyctophilus* (Chiroptera: Vespertilionidae) from Lembata Island, Nusa Tenggara, Indonesia. *Rec. West. Aust. Mus.* **15**, 97–107.
- KOOPMAN, K. F. (1984): A synopsis of the families of bats. Part VI. *Bat Research News* **25**, 15–17.
- LAURIE, E. M. O.; HILL, J. E. (1954): List of land mammals of New Guinea, Celebes and adjacent islands 1758–1952. London: British Museum (Nat. Hist.).
- MENU, H. (1987): Morphotypes dentaires actuels et fossiles des Chiropteres Vespertilionines. 2eme partie: Implications systematiques et phylogenetiques. *Palaeovertebrata* **17**, 77–150.
- MILLER, G. S. (1907): The families and genera of bats. *Bull. U.S. Nat. Mus.* **57**, 1–282.

- RUEDAS, L. A.; LEE, T. E.; BICKHAM, J. W.; SCHLITZER, D. A. (1990): Chromosomes of five species of vespertilionid bats from Africa. *J. Mammalogy* 71, 94–100.
- SIBLEY, C. G.; AHLQUIST, J. E. (1985): The phylogeny and classification of the Australo-Papuan passerine birds. *Emu* 85, 1–14.
- STRAHAN, R. (ed.) (1983): Complete book of Australian Mammals. London, Sydney, Melbourne: Angus and Robertson.
- TATE, G. H. H. (1942): Results of the Archbold expeditions No. 47. Review of the vespertilionine bats, with special attention to genera and species of the Archbold collections. *Bull. Amer. Mus. Nat. Hist.* 80, 221–297.
- TIDEMANN, C. R. (1986): Morphological variation in Australian and island populations of Gould's Wattled Bat, *Chalinolobus gouldii* (Gray) (Chiroptera: Vespertilionidae). *Aust. J. Zool.* 34, 503–514.
- TROUGHTON, E. LE G. (1943): Furred animals of Australia. Sydney: Angus and Robertson.
- VOLLETH, M. (1987): Differences in the location of nucleolus organizer regions in European vespertilionid bats. *Cytogenet. Cell Gen.* 44, 186–197.
- (1989): Karyotypevolution und Phylogenie der Vespertilionidae (Mammalia: Chiroptera). Diss., Univ. Erlangen-Nürnberg.
- VOLLETH, M.; TIDEMANN, C. R. (1989): Chromosome studies in three genera of Australian vespertilionid bats and their systematic implications. *Z. Säugetierkunde* 54, 215–222.
- ZIMA, J.; CERVENY, J.; HORACEK, I.; MACHOLAN, M.; VOLLETH, M. (1991): Karyotypes of two species of bats, *Otonycteris hemprichi* and *Pipistrellus trautatus* (Chiroptera: Vespertilionidae). In: Prague studies in mammalogy. Ed. by I. HORACEK and V. VOHRALIK. Prague: Charles Univ. Press. (In press).

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